

Foregut anatomy of the Cochlespirinae (Gastropoda, Conoidea, Turridae)

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ABSTRACT

The foregut anatomy of 20 species, belonging to eight genera, of the subfamily Cochlespirinae is described. A cladistic analysis based on several most important characters (morphology of proboscis, position of buccal sphincters, histology of venom gland, position of the venom gland opening, structure of muscular bulb, and morphology of radular teeth) revealed three more or less well-defined groups within the subfamily. The main feature characterizing the subfamily as a whole and separating groups within it, appeared to be the structure of venom gland and its muscular bulb. The subgenus *Sibogasyrinx* of the genus *Leucosyrinx* was shown to deserve a genus status. Some genera appeared to be intermediate between Cochlespirinae and Crassispirinae in some anatomical characters, and their taxonomic position remains not completely clear.

KEY WORDS

Cochlespirinae,
Conoidea,
anatomy,
foregut,
histology.

RÉSUMÉ

L'anatomie du système digestif des Cochlespirinae (Gastropoda, Conoidea, Turridae).

L'anatomie du système digestif de 20 espèces, appartenant à huit genres de la sous-famille Cochlespirinae, est étudiée. Une analyse cladistique, fondée sur les plus importants caractères de ce groupe (la morphologie de la trompe, la disposition des sphincters, l'histologie de la glande à venin, la disposition de l'ouverture de la glande à venin, la structure de la poire musculaire et la morphologie des dents de la radula) a permis de distinguer trois groupes plus ou moins homogènes. Le caractère principal, qui permet de caractériser la sous-famille et de la diviser en différents groupes morphologiques, est la structure de la glande à venin et de sa poire musculaire. Le sous-genre *Sibogasyrinx* du genre *Leucosyrinx* mérite le statut de genre. Quelques genres semblent occuper une position intermédiaire entre les deux sous-familles Crassispirinae et Cochlespirinae, et leur position taxonomique n'est pas encore définitivement établie.

MOTS CLÉS

Cochlespirinae,
Conoidea,
anatomie,
système digestif,
histologie.

INTRODUCTION

The superfamily Conoidea is well-defined morphologically due to the presence of venom gland and highly modified radular teeth. At the same time the relationships within the superfamily are still far from being clear, and this is one of the main problems of the current taxonomy of the group.

Investigations of phylogenetic relations within Conoidea and the classification of the superfamily were mainly based on characters of shell and radula (e.g., Powell 1966; McLean 1971), and only recent studies have paid much attention to the anatomy of digestive system, which is the most variable and, therefore, the most informative division.

The first comprehensive analysis of conoidean anatomy together with radula and shell morphology was published in 1993 (Taylor *et al.* 1993). This demonstrated the importance of anatomical characters for taxonomic and phylogenetic analysis of the group. Although this study was based on the anatomy of 72 species, this is still only a small portion of living species of the superfamily (apparently no less than 5000 species).

In anatomical studies of Conoidea, the very diverse family Turridae is of a special interest. The family consists of four currently recognized subfamilies, *viz* Turrinae, Clavatulinae, Crassispirinae, and Cochlespirinae, and is characterized by a radula with a membrane and marginal teeth usually of wishbone type (Taylor *et al.* 1993). The taxonomic position of many representatives of this family and their placement in the subfamilies are still controversial.

Anatomical study of the subfamily Crassispirinae (Kantor *et al.* 1997) has shown many interesting features and has allowed a clearer definition of the boundaries of the subfamily. This work has made evident the necessity of similar studies devoted to other subfamilies, for the complete analysis of relationships among Turridae and more reliable separation of subfamilies.

Therefore, the aim of the present study was to analyze the anatomy of species of the subfamily Cochlespirinae and to reveal the morphological diversity of its representatives with the objective

of establishing relationships of this subfamily with other taxa of Turridae.

MATERIAL AND METHODS

The subfamily Cochlespirinae is considered to include 22 Recent genera (Taylor *et al.* 1993). The present study covers eight of them, as well as two genera (*Kurilohadalia* Sysoev & Kantor, 1986 and *Plicisyrinx* Sysoev & Kantor, 1986), which were previously assigned to Crassispirinae (Taylor *et al.* 1993). The two latter genera cannot be actually included in Crassispirinae (Kantor *et al.* 1997), and therefore they are presently considered in Cochlespirinae, within which they were originally described (Sysoev & Kantor 1986).

The study of anatomy of Cochlespirinae was based on 20 species from the Pacific and the Atlantic, collected from depths of 100 to 7000 m (Table 1).

The anatomy was studied from longitudinal serial sections of the foregut, cut at 10 μ m and stained in Mason's triple stain. The radula was examined by SEM. In some cases, the results of hand dissections were also used.

The character analysis was performed using PAUP version 3.1.1 (Swofford 1993).

ABBREVIATIONS USED IN THE FIGURES

bc	buccal cavity
blp	buccal lips
bm	buccal mass
bt	buccal tube
btsa	anterior sphincter of buccal tube
btss	shifting sphincter of buccal tube
cm	columnellar muscle
con	circumoesophageal nerve ring
ctl	connective tissue layer of muscular bulb
cbt	sac-like enlargement of buccal tube
ech	rhynchodeum epithelium change
eoc	oesophagus enlargement
ep	epithelial pad
gre	glandular part of rhynchodeum
mb	muscular bulb
oe	oesophagus
pb	proboscis
pw	proboscis wall
rhc	rhynchocoel
rhs	rhynchostomal sphincter
rhw	rhynchodeum wall

TABLE 1. — List of cochlespirine species, which have been sectioned, with details of their collection location.

The additional material included sections of *Megasurcula carpenteriana* (Gabb, 1865), *Aforia inoperculata* Sysoev & Kantor, 1988, *A. circinata* (Dall, 1873), *A. lepta* (Watson, 1881), *A. moskalevi* Sysoev & Kantor, 1987, *A. aulaca alaskana* Sysoev & Kantor, 1987, *A. crebristriata* (Dall, 1908), *A. abyssalis* Sysoev & Kantor, 1987, *A. kupriyanovi* Sysoev & Kantor, 1987, kindly provided to the author by John Taylor (the first species) and Yuri Kantor (all other species).

Species	Campaign	Station	Depth	Location	Coordinates
<i>Antiplanes sanctioannis</i> (Smith, 1875).	R/V <i>Gidronavt</i>	dredge No. 41	110 m	Paramushir Id., Pacific side	50°15'N, 156°29'E
	R/V <i>Gidrobiolog</i>	stn 124	550 m		48°15'N, 140°41'E
<i>Carinoturris polycaste</i> (Dall, 1919)	R/V <i>Vityaz</i>	stn 4179	1258 m	North California	42°40' N, 125°00' W
<i>Cochlespira pulchella</i> (Schepman, 1913)	R/V <i>Baruna Jaya</i> , KARUBAR	stn CP 59	405-399 m	Indonesia, Tanimbar Is.	08°20'S, 132°11'E
<i>Cochlespira radiata</i> (Dall, 1889).	R/V <i>Marion Dufresne</i> , MD55	stn CP 11	248-262 m	SE Brazil	23°35'S, 40°06'W
<i>Comitas murrayolga</i> (Garrard, 1961)	R/V <i>Vauban</i> , MUSORSTOM 4	stn DW 229	445-460 m	Southern New Caledonia	22°52'S, 167°13'E
<i>Comitas onokeana vivens</i> Dell, 1956	R/V <i>Dmitry Mendeleev</i>	stn 1269, Sigsbee trawl	720 m		14°26'S, 174°29'W
<i>Kurilohadalla elongata</i> Sysoev & Kantor, 1986. Zoological Museum of Moscow State University Lc-22398, paratype	R/V <i>Vityaz</i>	stn 2208	7210-7230 m	Kurile-Kamchatka trench, east of North Kurile Is.	49°29'N, 158°41'E
<i>Leucosyrinx (Sibogasyrinx)</i> <i>pyramidalis</i> (Schepman, 1913)	R/V <i>Baruna Jaya</i> , KARUBAR	stn CP 72	699-676 m	Indonesia, Tanimbar Is.	08°36'S, 131°33'E
<i>Leucosyrinx verrilli</i> (Dall, 1881)	R/V <i>Akademik Kurchatov</i> , 14th cruise	stn 1209	1060 m	NE Atlantic	13°04'N, 63°06'W
<i>Marshallena philippinarum</i> (Watson, 1882)	R/V <i>Coriolls</i> , BIOGEOCAL	stn CP 260	1820-1980 m	Loyalty Basin	21°00'S, 166°58'E
<i>Plicisyrinx decapitata</i> Sysoev & Kantor, 1986. Zoological Museum of Moscow State University Lc-22388, paratype	R/V <i>Vityaz</i>	stn 3166	5557 m	E South Kurile Is.	44°42,09'N, 153°49'E

rs	radular sac
rso	radular sac opening
rst	rhynchostome
sg	salivary gland
sgd	salivary gland duct
st	proboscis stalk
vg	venom gland
vgd	venom gland duct

HISTORICAL REVIEW OF COCHLESPIRINAE AND THE PRESENT CONCEPT OF THE SUBFAMILY

The subfamily Cochlespirinae with the type genus *Cochlespira* Conrad, 1865 was established by Powell (1942) for a group of fossil and Recent genera characterized by a "thin fusiform shell, with sharp, sometimes frilled, peripheral keel" (Powell 1942: 31). Subsequently Powell (1966) has synonymized Cochlespirinae with Turriculinae Powell, 1942 because of slight differences between the subfamilies. According to Powell's (1966, 1969) concept of Turriculinae, the subfamily was rather heterogeneous and included genera with different styles of radula, but united by moderate to large shell size, more or less narrowly fusiform shape, the sinus position on the shoulder, a tall spire, and a long canal.

McLean (1971) generally employed Powell's concept of Turriculinae, but restricted the subfamily to genera with a uniform type of radula, consisting of wishbone marginal teeth and a variously developed (to absent) central tooth. In the revision of Conoidea based on anatomical characters (Taylor *et al.* 1993), the authors found that the type genus of the subfamily, *Turricula* Schumacher, 1817, is very close anatomically to representatives of the subfamily Clavatulinae Gray, 1853. Therefore, *Turricula* was transferred to Clavatulinae and Turriculinae became a synonym of the latter. This made the name Cochlespirinae valid for the group consisting of the rest of Turriculinae sensu Powell. The diagnosis of Cochlespirinae in Taylor *et al.* mainly followed that of earlier authors and was mainly based on conchological characters, because anatomical data did not give sufficient grounds for the clear separation of Cochlespirinae from, for example, Crassispirinae McLean, 1971. There-

fore, 22 Recent genera (and 6 subgenera) recognized by Taylor *et al.* (1993) in Cochlespirinae, were characterized by the following set of conchological features: shell of medium to large size, fusiform or pagodiform, with usually moderately elongate canal, generally deep anal sinus on the shoulder, and usually multispiral and smooth (at least initially) protoconch.

ANATOMY

This section describes anatomy of the anterior part of the digestive system and radula of each species. Unfortunately, many species were represented by a single specimen, therefore the radula descriptions are given only for some species. Besides the original material, we used the data on the anatomy of *Aforia* spp. (Sysoev & Kantor 1987, 1988), with some additions and corrections based on the study of original preparations. Detailed descriptions of these species are given in the respective papers, and some corrections are listed in Table 3.

Cochlespira pulchella (Schepman, 1913) (Figs 1; 16A, B)

As the anatomy of *C. radiata* (Dall, 1889) (Fig. 16C) differs only slightly from that of *C. pulchella*, the description mostly concerns both species, with the differences being specially indicated.

The rhynchodeum is narrow and long. The rhynchodeal sphincter is large, in posterior position. The change of glandular epithelium occurs in the first third of the rhynchodeum length in inverted position. The entire part of rhynchodeum covered by epithelium similar to that of proboscis, is evertible.

The proboscis is long, with a rather large basal diameter and narrowing apically. At the apical end of proboscis there are two anterior sphincters with a sac-like buccal enlargement between them and a medium-sized epithelial pad. The buccal tube is almost straight in the apical part, and with regular small folds in the basal part. The lumen of the buccal tube is rather narrow and

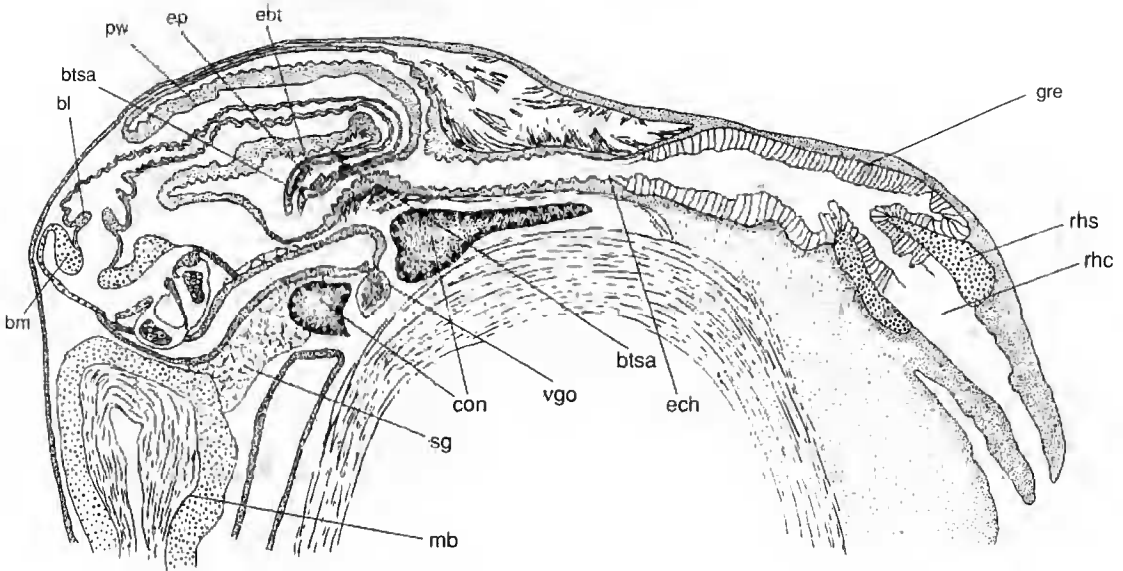


FIG. 1. — *Cochlespira pulchella*, reconstruction based on longitudinal sections through the foregut.

expands greatly in front of the buccal mass. Proboscis and buccal tube walls are rather muscular, at the base the proboscis wall thickness is about 19% of the total proboscis diameter, the buccal tube wall thickness is about 6%.

The buccal mass is large, muscular, and situated posterior to the proboscis. Buccal lips are rather long, muscular, and inverted. The buccal mass forms a caecum-like structure with the opening of radular sac. In *C. radiata* it is better developed. The radular sac has a wide opening, and the buccal sac is absent.

Ducts of salivary glands are long and open on both sides of radular sac. Salivary glands are very large and acinous. The venom gland opens under the nerve ring and behind the buccal mass. The histology of the venom gland does not change posterior to the nerve ring. The muscular bulb is very large (small in *C. radiata*), comprised by two oppositely oriented layers of muscles, and without a connective tissue layer. The lumen of the muscular bulb is rather narrow. The oesophageal loop is very long. The buccal mass is situated anteriorly, far from the nerve ring. The oesophagus diameter does not change markedly behind the nerve ring.

The anatomy of *Cochlespira radiata* and *C. pulchella* differs only in small details. The radula of both species has a well-formed central tooth with a strong central cusp. Marginal teeth of *C. pulchella* (Fig. 16A, B) are of the wishbone type with two limbs. Teeth of *C. radiata* (Fig. 16C) appear to be longitudinally folded and somewhat twisted, with a central channel.

Leucosyrinx verrilli (Dall, 1881)
(Fig. 2)

The large rhynchodeum sphincter lies in an anterior position and practically encircles the rhynchostome. The epithelium of the rhynchodeal wall is glandular and changes histology in the posterior quarter of the rhynchodeum length. The posterior part of the rhynchodeum is lined by an epithelium similar to that of proboscis. It is evertible.

The proboscis is of medium length, with a rather large diameter, with the apical end loosely coiled inside the rhynchodeum. At the tip of proboscis, there are two anterior sphincters and a sac-like buccal enlargement between them. A well-developed epithelial pad is situated in front of the

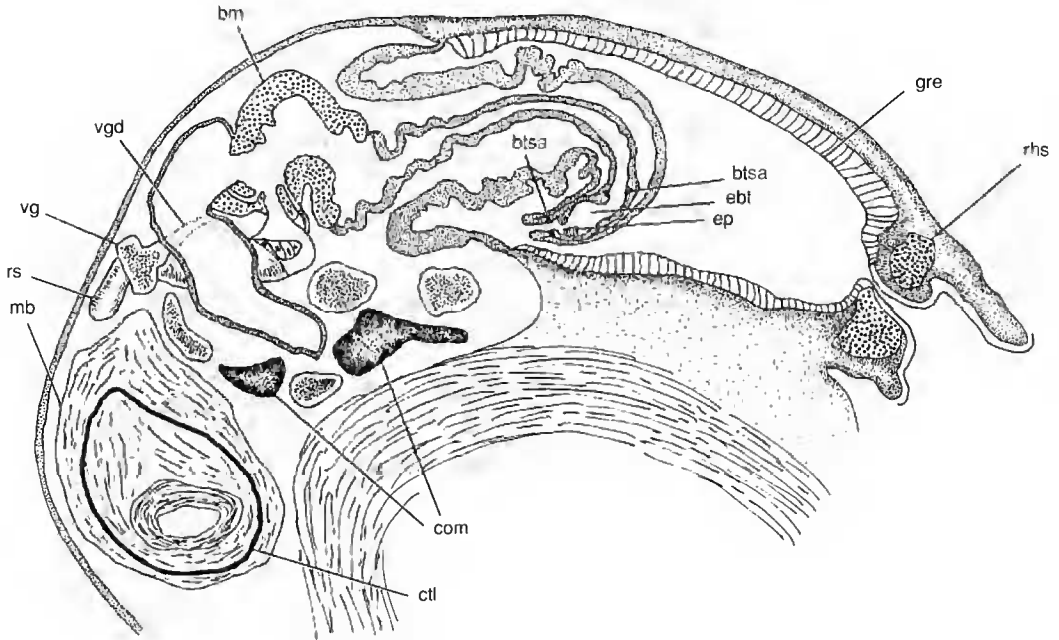


Fig. 2. — *Leucosyrinx verrilli*, reconstruction based on longitudinal sections through the foregut.

first sphincter. The buccal tube is straight. Proboscis walls are not very muscular and uniformly thin along their entire length. The wall thickness is about 7% of the total proboscis diameter and the buccal tube wall thickness is about 6%.

The buccal mass is medium-sized, muscular and situated posterior to the proboscis. Buccal lips are absent. The radular sac opening is rather narrow and the buccal sac is absent. Ducts of the salivary glands are rather short, weakly coiled and open on both sides of radular sac. Salivary glands are very small and acinous. The venom gland opens at the boundary of buccal mass by a small duct. Venom gland histology is unchanged posteriorly. The muscular bulb is composed of two layers of longitudinal muscles separated by a layer of unstructured connective tissue, with an innermost layer of circular fibres. The muscular bulb lumen is rather narrow. The oesophagus is greatly looped. The oesophagus diameter does not markedly increase behind the nerve ring. Data on radula are absent.

Leucosyrinx (Sibogasyrinx) pyramidalis
(Schepman, 1913)
(Figs 3; 16D, E)

The large rhynchodeal sphincter is anterior and almost encircles the rhynchostome. The epithelium of the rhynchodeal wall is glandular, changes histology in the rear quarter of the rhynchodeum length. The posterior part of the rhynchodeum is lined by an epithelium similar to that of proboscis. It is evertible.

The proboscis is long, with rather a large basal diameter; the apical end is very narrow, rolled up into a ball. At the proboscis tip there are two anterior sphincters and a sac-like buccal enlargement between them. A distinct epithelial pad is absent. The buccal tube is straight apically and folded basally, with a narrow lumen. It greatly expands in front of the buccal mass. Proboscis and buccal mass walls are weakly muscular and thin. In the apical part the wall thickness is slightly more than 10% of the total proboscis diameter, whereas the buccal tube wall thickness

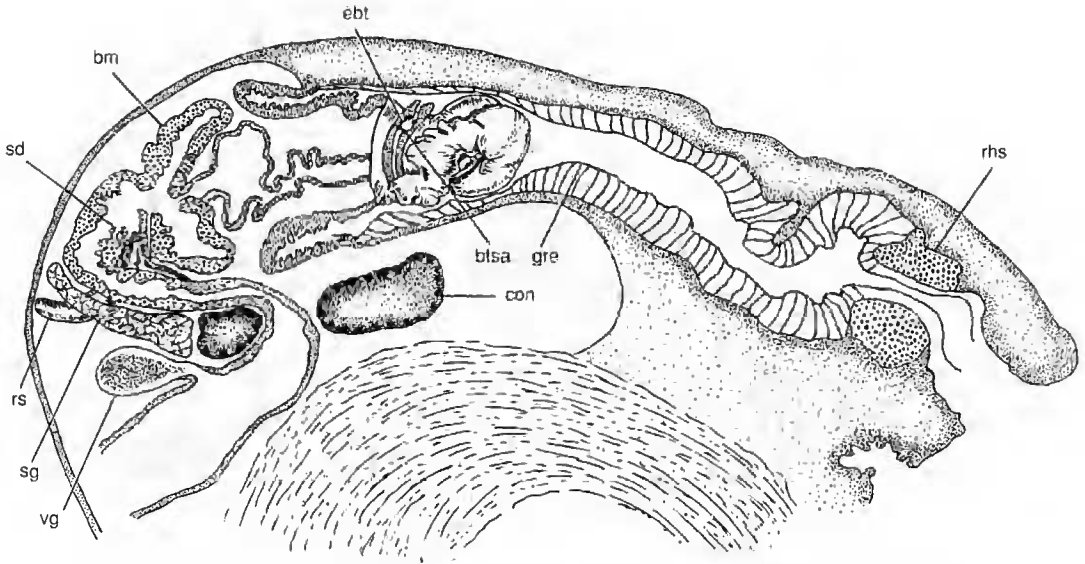


FIG. 3. — *Leucosyrinx* (*Sibogasyrinx*) *pyramidalis*, reconstruction based on longitudinal sections through the foregut.

is only about 4%. The proboscis diameter greatly increases basally, with a corresponding increase in the wall thickness, whereas the buccal tube walls remain thin-walled, and their thickness becomes only about 2-3% of the total proboscis diameter. The buccal mass is large, weakly muscular, curved and situated behind the proboscis. Buccal mass walls are thin, with hardly differentiated end of buccal mass, because the histology of the oesophageal wall does not differ from that of buccal mass. The difference consists only in the relative thickness of muscle layers and walls themselves. Buccal lips are long, inverted and rather muscular.

The radular sac has a wide opening and lacks a buccal sac. Ducts of salivary glands are long and open on both sides of radular sac. Salivary glands are medium-sized and acinous. The venom gland opens into the oesophagus beyond the buccal mass, behind the nerve ring (therefore, it does not pass through the nerve ring). The duct is absent. Venom gland histology does not change. The muscular bulb is composed of two opposing layers of muscles, without a connective tissue layer. The lumen of muscular bulb is rather narrow. The oesophagus is moderately elongated. The buccal mass is situated not far anteriorly of

the nerve ring. The oesophagus diameter greatly increases behind the nerve ring.

The radula (Fig. 16D, E) is very similar to that of *Cochlespira pulchella*, having wishbone marginal teeth and a well-defined central tooth with a strong cusp.

Comitas onokeana vivens Dell, 1956
(Figs 4; 5A, B; 17A)

The rhynchodeal sphincter is small, anterior and situated slightly behind the rhynchostome. The rhynchodeum wall epithelium is glandular, differing from that of proboscis wall. The rhynchodeum is not evertible.

The proboscis is long, wide, straight and covered by regular small folds along the entire length. The structure of the proboscis tip is very peculiar. The muscular wall of proboscis becomes abruptly very thin and simultaneously the external epithelium changes from high columnar to very low. No distinct change of epithelium occurs at the apical end of proboscis. The external epithelium is the same as the internal buccal tube epithelium.

In the two sectioned specimens (Fig. 5A, B), the extent of eversion is different. In the place where

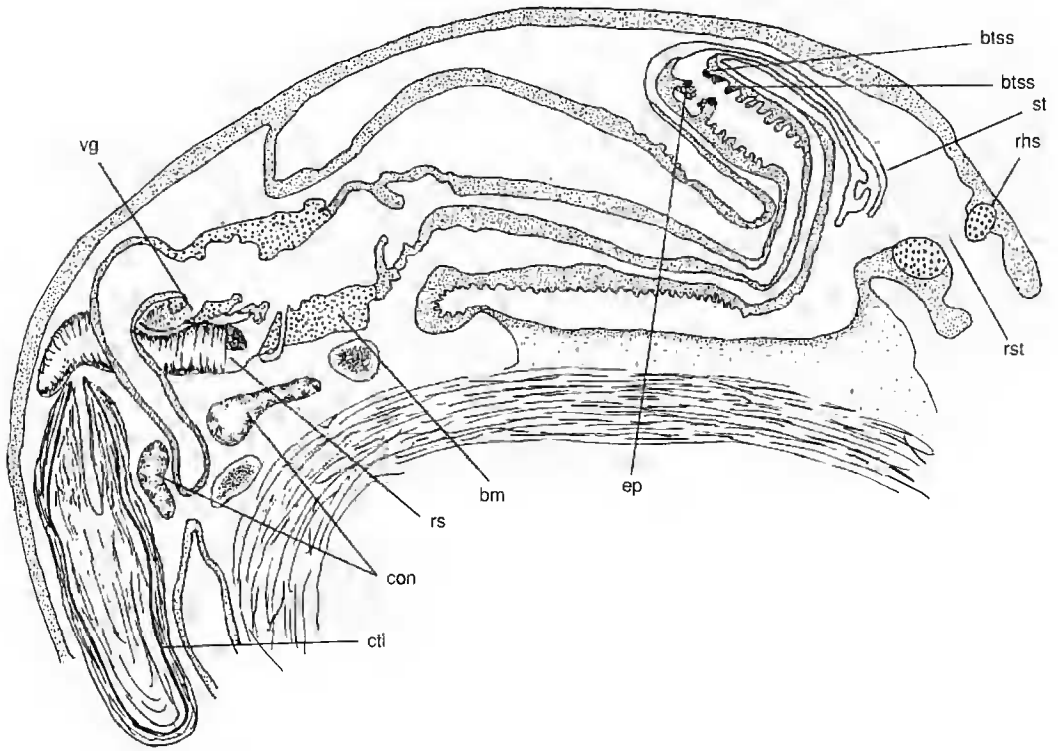


Fig. 4. — *Comitas onokeana vivens*, reconstruction based on longitudinal sections through the foregut.

the buccal tube becomes more muscular, there are two small sphincters on both sides of buccal sac-like enlargement. There are two glandular pads in the enlargement.

Morphologically, the structure of this portion corresponds to that of apical end of the proboscis with two anterior sphincters. It is seen (Fig. 5B) that the buccal tube may evert to such extent that this portion appears practically at the very end of the proboscis.

The buccal tube has small densely arranged folds along its entire length. Proboscis walls are not very muscular, with the same thickness along their entire length. The wall thickness is about 6-7% of the total proboscis diameter, the buccal tube wall thickness about 10%. The buccal tube is lined with rather low columnar epithelium, and becomes larger after beginning of buccal mass. The oesophagus is lined with columnar epithelium. The buccal mass is rather large, mus-

cular and situated behind the proboscis. Buccal lips are absent. The oesophageal wall forms not muscular, rather long but thin lips in front of the buccal mass.

The radular sac has a wide opening, whilst the buccal sac is absent. Ducts of the salivary glands are rather long and coiled, and open on both sides of radular sac. Salivary glands are small and acinous. The venom gland opens near the radular sac, at the posterior part of the buccal mass. The duct is absent. Venom gland histology does not change. The muscular bulb is composed of two layers of longitudinal muscles separated by a layer of unstructured connective tissue. The outer layer thickness is three to four times more than that of inner layer. The lumen of the muscular bulb is rather large. The oesophagus is moderately elongated. The oesophageal diameter does not increase behind the nerve ring.

The radula (Fig. 17A) consists of flat marginal

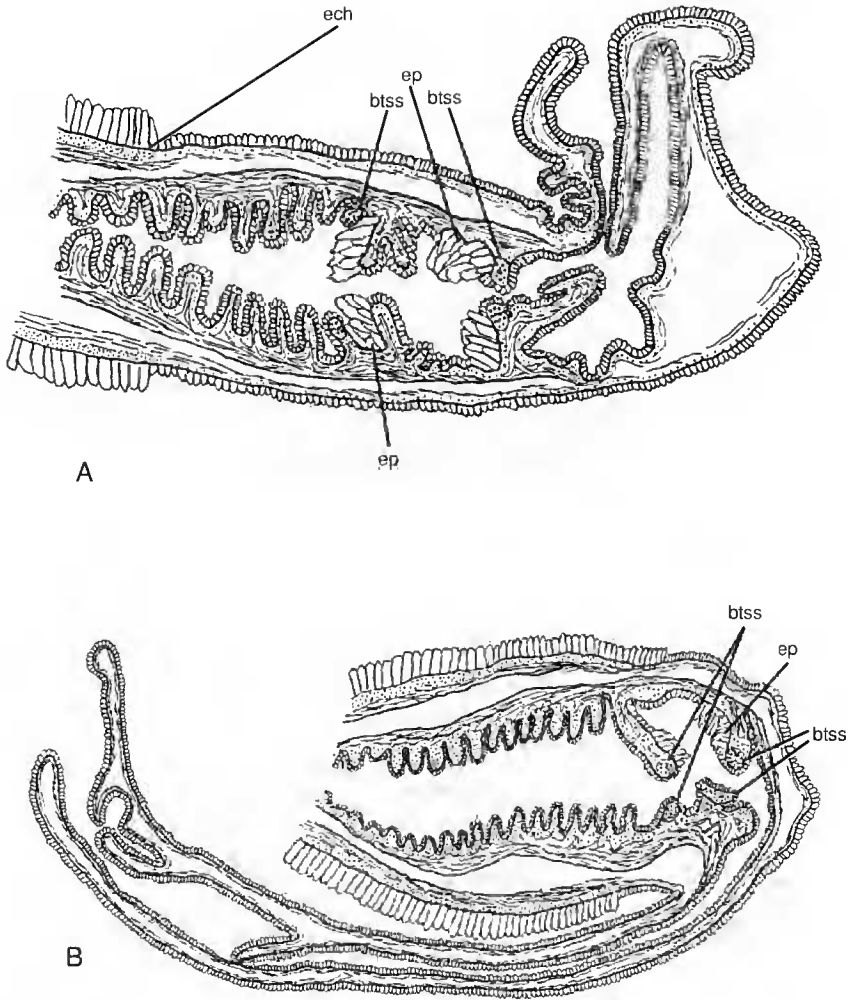


FIG. 5. — A, B, *Comitas onokeana vivens*, reconstruction based on longitudinal sections through the apical part of the proboscis, different extent of the eversion.

teeth thickened on the outer sides, with two flat plates in the central part.

Comitas murrawolga (Garrard, 1961)
(Fig. 17B, C)

The anatomy of *Comitas murrawolga* and *C. onokeana vivens* differs only in minor details. *C. murrawolga* has very small buccal lips inverted into the buccal cavity. Marginal teeth are very similar to those of *C. onokeana vivens*, but

C. murrawolga has also a distinct central tooth instead of two flat plates.

Antiplanes sanctioannis (Smith, 1875)
(Fig. 6A, B)

The rhynchodeal sphincter is anterior. The epithelium of the rhynchodeal wall is glandular and differs from that of proboscis wall. The proboscis is long, wide, straight and covered by regular small folds along its entire length. The structure

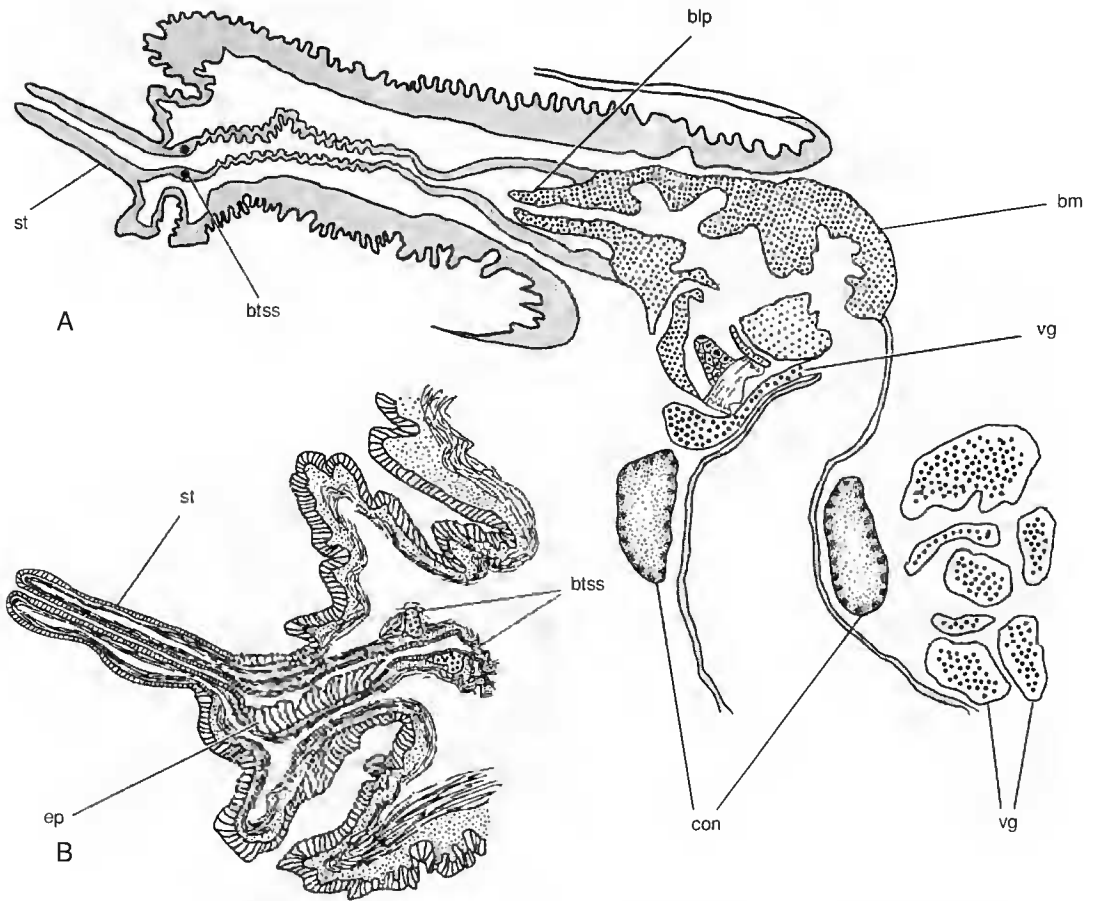


FIG. 6. — *Antiplanes sanctioannis*. **A.** reconstruction based on longitudinal sections through the foregut; **B.** apical part of proboscis.

of the proboscis tip is similar to that of *Comitas*. The rather muscular wall of the proboscis becomes abruptly very thin, but, in contrast to *Comitas*, without a change in outer epithelium. The anterior end of the proboscis is truncated apically, with a rather long and narrow stalk near the center of flattened area. No distinct change of epithelium occurs at the tip of the proboscis. In the two sectioned specimens, the extent of eversion is different. In the second specimen (not figured) the thin-walled portion is considerably shorter, and the buccal mass is situated behind the proboscis.

At the beginning of the wide portion of the proboscis there are a small sphincter and a sac-like

buccal enlargement with a long and tall epithelial pad. The situation is thus similar to that in *Comitas*, where the structure of this part corresponds morphologically to that of the proboscis tip, whereas this part is intermediate in its position. The buccal tube has small densely arranged folds along its entire length.

The proboscis walls are rather muscular, with the same thickness along their entire length. The wall thickness is about 10-12% of the total proboscis diameter, whilst the buccal tube wall thickness is about 7-8%. The buccal tube is lined with a rather low columnar epithelium, becoming taller after the beginning of buccal mass. The oesophagus is lined with columnar epithelium.

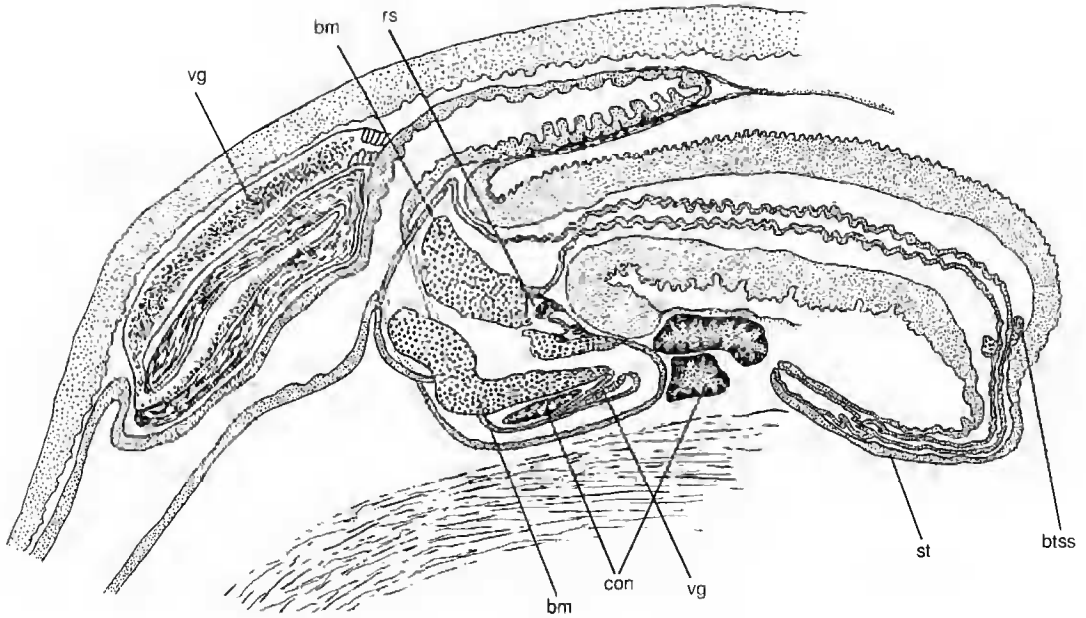


FIG. 7. — *Marshallena philippinarum*, reconstruction based on longitudinal sections through the foregut.

The buccal mass is large, muscular, folded and situated at the proboscis base. Buccal lips are long, thin, rather muscular and not everted. The radular sac has a wide opening, whilst the buccal sac is absent. Salivary ducts are long, coiled, open on both sides of radular sac. Salivary glands are large and acinous. The venom gland opens near the radular sac, at the rear boundary of buccal mass. A duct is absent. Venom gland histology does not change. The muscular bulb is composed of two layers of longitudinal muscles separated by a layer of unstructured connective tissue. The thickness of the outer layer is slightly less than that of the inner. The lumen of the muscular bulb is small. The oesophageal loop is short. Oesophagus diameter greatly increases behind the nerve ring.

The radula consists of two marginal teeth, composed of two flat plates.

Marshallena philippinarum (Watson, 1882)
(Figs 7; 17D, E)

The rhynchodeal sphincter is located in an anterior position. The epithelium of the rhynchodeal

wall is glandular, but is developed only in the anterior part of rhynchodeum. The rhynchodeum walls are very thin in the basal part, and the glandular epithelium is represented only by scattered cells. The rhynchodeum is not eversible.

The proboscis is long, straight, except the apical part, and of a small diameter which does not change along the proboscis length. The structure of the proboscis tip is similar to that of *Antiplanes*. The muscular wall of proboscis gradually becomes very thin without a change in the external epithelium. The proboscis walls are very thin in the apical part. At the beginning of the wide portion of the proboscis there is a large sphincter, whereas a sac-like buccal enlargement and epithelial pad are absent. The buccal tube is rather strongly coiled inside the proboscis. Proboscis walls are muscular in the basal part. The wall thickness is about 19% of the total proboscis diameter, with the buccal tube wall thickness about 3-4%.

The buccal mass is very large and muscular. It is situated almost perpendicular to the proboscis and bent so that its end lies almost at the probos-

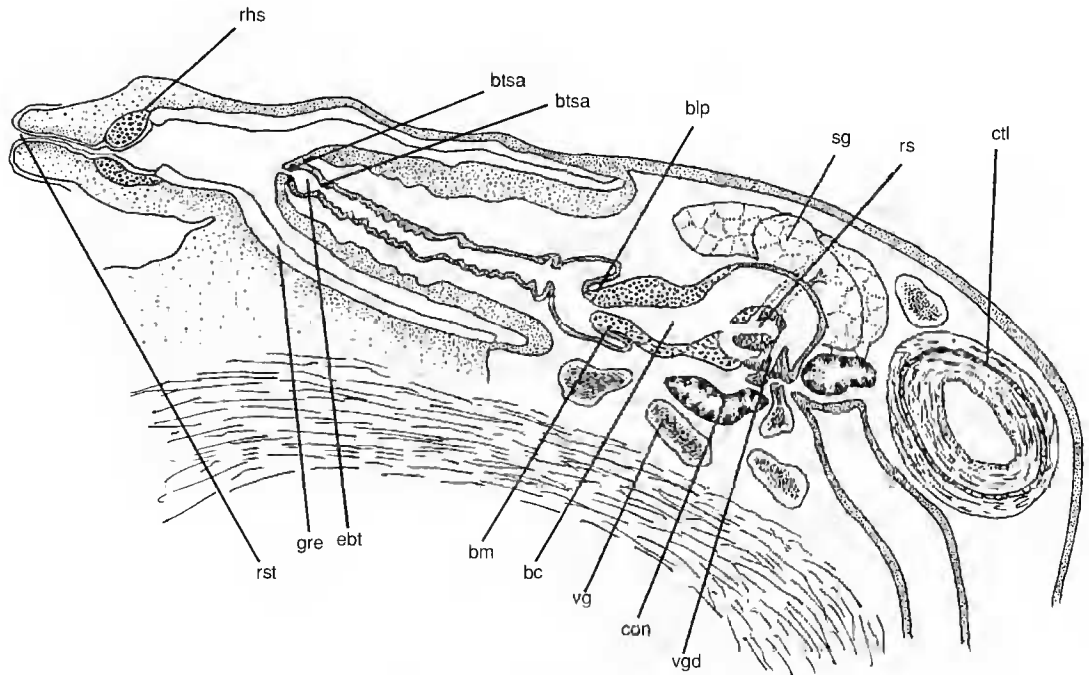


FIG. 8. — *Kurilohadalia elongata*, reconstruction based on longitudinal sections through the foregut.

cis base. In Figure 7 the buccal mass is shown at a slightly reduced scale. The nerve ring lies almost immediately behind the buccal mass, near the proboscis base. Buccal lips are rather short but muscular, and not everted. The radular sac is very short, with a narrow opening, the buccal sac is absent.

The salivary ducts are long, slightly coiled and open on both sides of radular sac. The salivary glands are large and acinous. (The glands and ducts are not shown in Figure 7). The venom gland opens far behind the radular sac, at the rear boundary of the buccal mass. The duct is absent. The histology of the venom gland is very different from usual. A hollow, uncoiled tube arises from the buccal mass, goes strictly along the oesophagus and passes through the nerve ring. It is lined with a glandular epithelium with very large cells, the venom granules are absent. The histology of the venom gland changes just in front of the muscular bulb. The epithelium abruptly disappears, and the tube becomes filled by venom granules. The granules are present also

in the lumen of the muscular bulb. The muscular bulb is composed of two layers of longitudinal muscles separated by a layer of unstructured connective tissue. The thickness of the outer layer is slightly less than that of the inner. The lumen of muscular bulb is small. The oesophagus is slightly elongated. Oesophagus diameter does not increase markedly behind the nerve ring, but the oesophagus forms an appendix, extending between the rhynchodeum wall and the body wall. The wall of oesophagus is almost fused with the thin wall of rhynchodeum. The epithelium of the oesophagus consists of very large cells, with a number of regularly arranged, large, glandular cells.

The radula (Fig. 17D, E) consist only of two marginal teeth in each row. The teeth are wish-bone and composed of two nearly equal limbs.

Kurilohadalia elongata Sysoev & Kantor, 1986
(Fig. 8)

The rhynchodeum sphincter is in the anterior

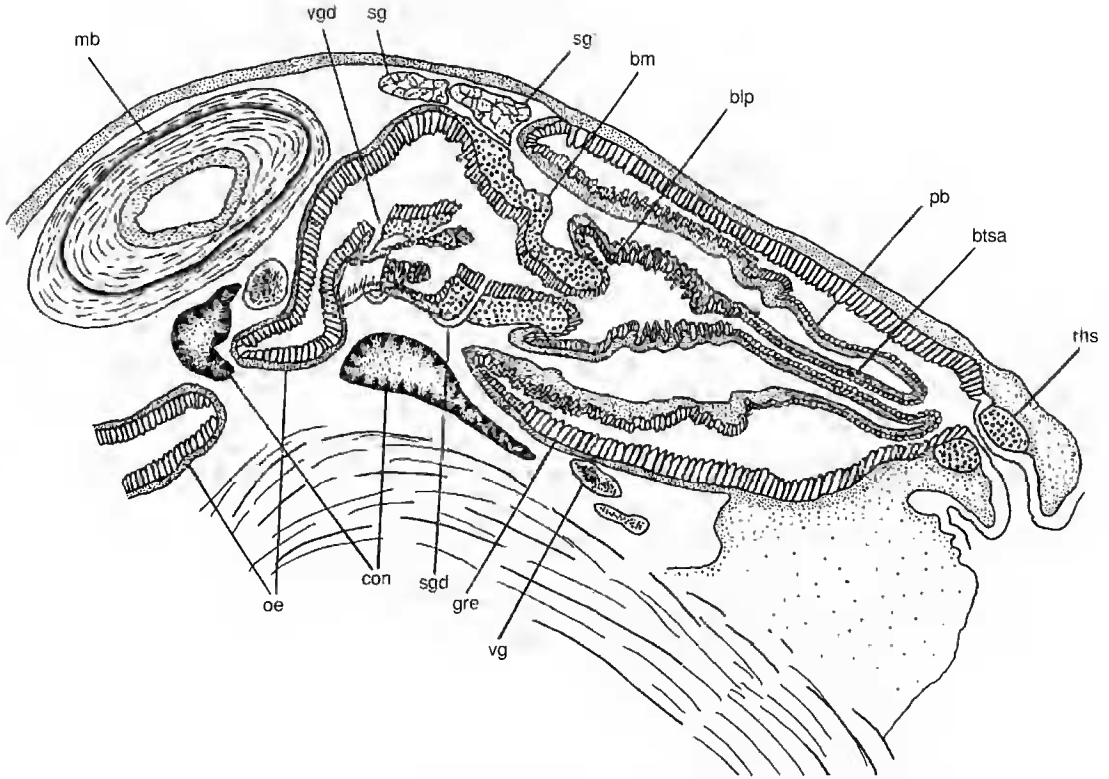


FIG. 9. — *Plicisyrinx decapitata*, reconstruction based on longitudinal sections through the foregut.

position but shifted backward. A glandular epithelium is present.

The proboscis is rather long, uncoiled and occupies most of the rhynchodeum. The proboscis diameter does not change along its length. The buccal tube is very narrow from the mouth to the first sphincter. At the tip of the proboscis there are two anterior sphincters, the first one being smaller than the second. There is a sac-like buccal enlargement between the sphincters. It is lined with a tall epithelium, differing from the rest of the buccal tube epithelium. Buccal tube walls are very thin and rather strongly folded inside the proboscis.

The proboscis diameter is very large, but the proboscis walls are not very muscular, the wall thickness being about 7% of the total diameter. The proboscis mostly consists of longitudinal muscles. The buccal mass is large, situated behind the proboscis. Buccal lips are long and very muscu-

lar, whilst the walls of the buccal mass are weakly muscular. In the radular sac opening there are thin and long lips. Salivary ducts are very short, straight and open into a deep buccal sac. Salivary glands are large, with an anastomosing-tubular morphology. The venom gland opens near the radular sac by a very short duct.

Venom gland histology does not change. The muscular bulb consists of two layers of large longitudinal muscle fibres separated by a very thin layer of structured connective tissue with a thin innermost layer of circular fibres. The lumen of muscular bulb is very broad. The oesophagus diameter does not increase markedly after the nerve ring.

The radula consists of two rows of marginal teeth only. The teeth are elongated, leaf-shaped, slightly curved in profile and consist of two flattened parts tightly adjoining each other (Sysoev & Kantor 1986).

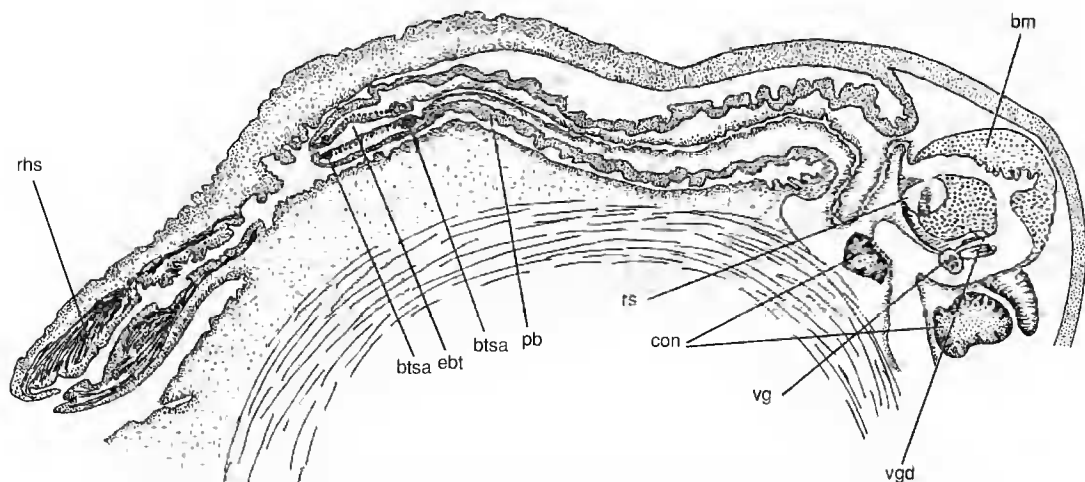


FIG. 10. — *Megasurcula carpenteriana*, reconstruction based on longitudinal sections through the foregut.

Plicisyrinx decapitata Sysoev & Kantor, 1986
(Fig. 9)

The rhynchodeum sphincter lies in the anterior position and shifted backward. The rhynchodeal wall epithelium differs from that of the proboscis wall. The rhynchodeum is not evertible.

The proboscis is long, with virtually the same diameter along its entire length, but the apical part is narrower. The sac-like buccal enlargement and epithelial pad are absent. The buccal tube sphincter is anterior, the distance from the mouth to the sphincter is slightly more than the tooth length. Teeth are very long. The walls of proboscis, buccal tube, and oesophagus are very thin. The proboscis wall thickness is about 5-6%, and buccal tube wall thickness is about 2% of the total proboscis diameter. The basal part of the proboscis is externally covered by a columnar epithelium with a thin cuticle. The apical part is covered by a cubic epithelium, also cuticulized, with a very even surface. The buccal tube is lined with a rather low columnar epithelium, which becomes larger after the beginning of buccal mass. The oesophagus is lined with a columnar epithelium without cilia.

The buccal mass is large, muscular, begins inside the proboscis and slightly coiled. Buccal lips are long and muscular. The radular sac opens outside the proboscis and the buccal sac is absent.

Salivary ducts are rather short, of small diameter, not very coiled, opening rather far from the radular sac, on both its sides, dorso-laterally and ventro-laterally. Salivary glands are very small and intermediate between acinous and tubular. This type of salivary glands was designated as modified acinous (Kantor *et al.* 1997). The venom gland opens near the radular sac, at the rear boundary of buccal mass. A very short duct is present. Venom granules appear near the gland opening. The venom gland histology does not change along its length. The muscular bulb is very large, consisting of two layers of large longitudinal muscle fibres separated by a layer of structured connective tissue, with a thin innermost layer of circular fibres. The lumen of the muscular bulb is very broad. The oesophagus is medium elongated. Oesophagus diameter does not increase posterior to the nervous ring. The radula consists of two rows of small, flattened, slightly curved, wishbone teeth (Sysoev & Kantor 1986).

Megasurcula carpenteriana (Gabb, 1865)
(Figs 10; 11)

The rhynchodeal sphincter is in the anterior position, very large. The sphincter is formed by longitudinal muscles. Longitudinal muscle bunches pass from the sphincter downward and

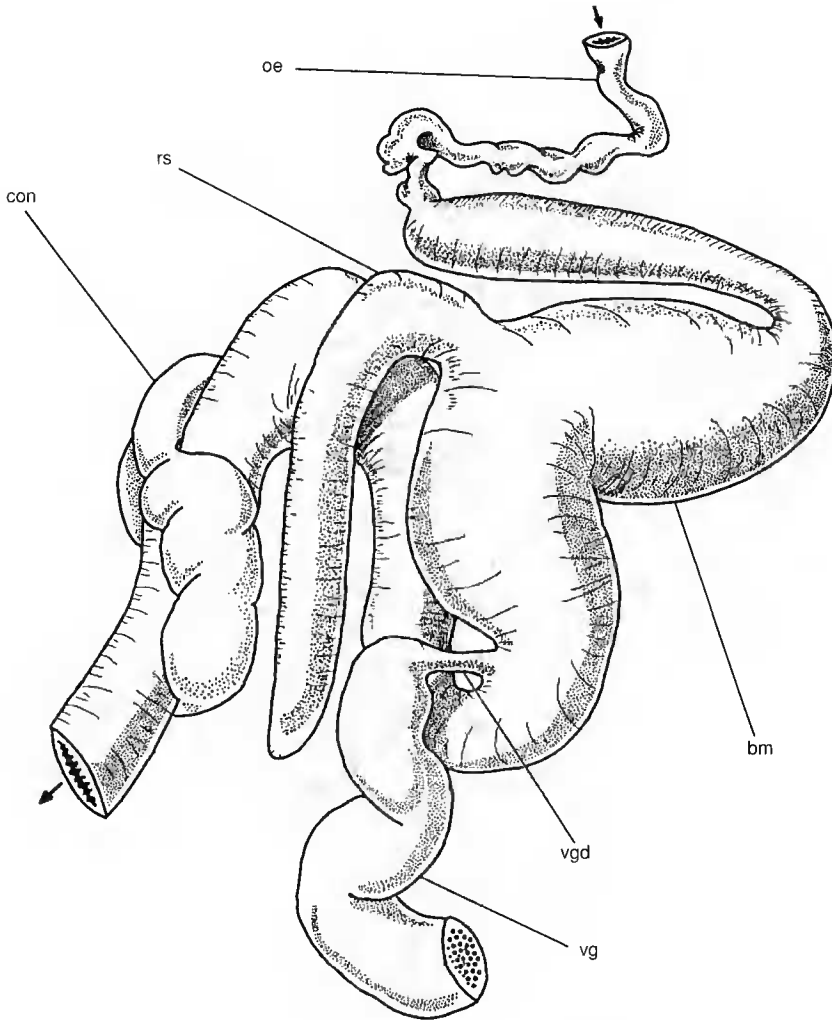


FIG. 11. — *Megasurcula carpenteriana*, buccal mass (reconstruction based on longitudinal sections through the foregut).

attach to the rhynchodeum wall. The rhynchodeum wall epithelium is not glandular. The rhynchodeum is not evertible.

The proboscis is long, wide and coiled inside the rhynchodeum. At the tip of the proboscis, there are two anterior sphincters and a sac-like buccal enlargement between them. The epithelial pad is absent. The buccal tube wall between the two sphincters is underlain by a layer of large circular fibres, i.e. there is a kind of long and thin sphincter. The buccal tube is folded, with very thin walls. Proboscis walls are rather muscular

and of the same thickness along the entire length. The wall thickness is about 9% of the total proboscis diameter and the buccal tube wall thickness is about 5%. Between the proboscis base and the beginning of buccal mass, the buccal tube is strongly coiled, very thin, and forms a rather long loop, which passes along the buccal mass like a wide and thin ribbon.

The buccal mass is large, very muscular, bent and situated outside of the proboscis. Buccal lips are absent. The radular sac has a wide opening, the buccal sac is absent. Salivary ducts are long,

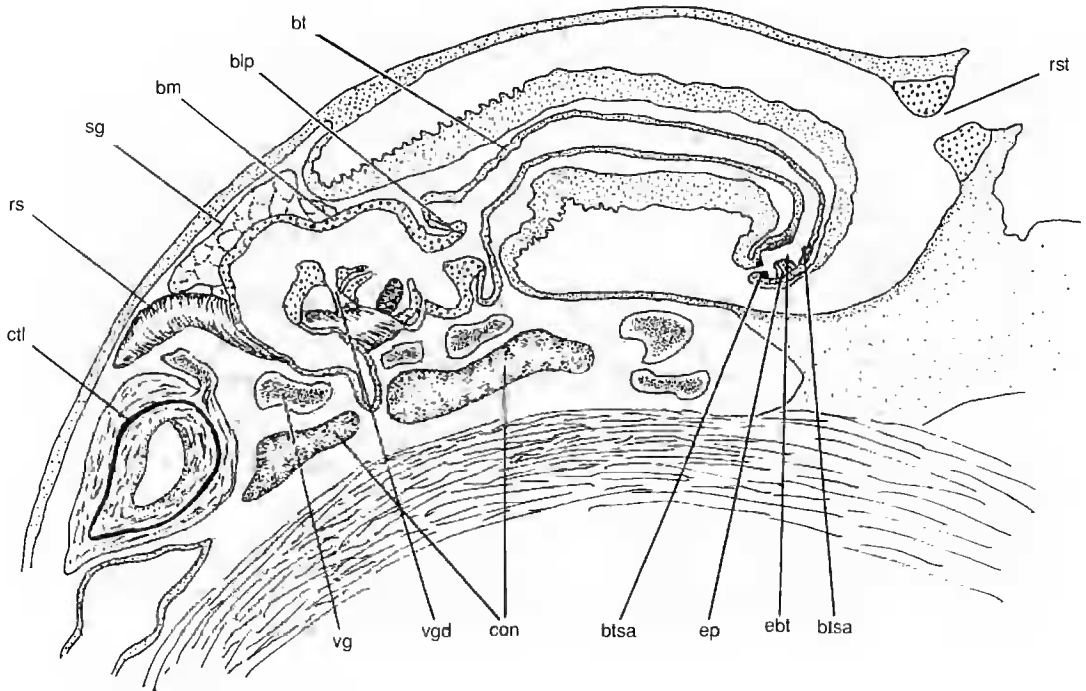


FIG. 12. — *Carinoturris polycaste*, reconstruction based on longitudinal sections through the foregut.

slightly coiled and open on both sides of radular sac. Salivary glands are large and acinous. The venom gland opens by a short duct at the border of buccal mass. The venom gland histology does not change along its length. The muscular bulb was not located on the slides. The elongation of oesophagus is well-expressed, the oesophagus forms a long loop near the buccal mass. The oesophagus diameter does not increase after the nerve ring.

Radular teeth are wishbone, with the distal limb of the base detached (Powell 1966).

Carinoturris polycaste (Dall, 1919)
(Fig. 12)

The rhynchodeum sphincter is in the anterior position, medium-sized, situated around the rhynchostome. The rhynchodeum wall epithelium differs from the proboscis wall external epithelium. The rhynchodeum is not evertible. The proboscis is long, with almost no change in

diameter along its length. The apical part is coiled inside the rhynchodeum. The buccal tube from the mouth to the first sphincter is very narrow. At the apical end of proboscis there are two anterior sphincters, the first one is very small, with a marked bend and a sac-like buccal enlargement behind it. The second sphincter is larger and situated behind the sac-like buccal enlargement. There is a large and very high epithelial pad within the enlargement. The proboscis wall thickness is about 20% of the total proboscis diameter, the buccal tube wall thickness is only about 4%. The buccal tube is lined with a rather low columnar epithelium, which becomes taller after the buccal mass beginning. The oesophagus is lined with a columnar epithelium.

The buccal mass is rather large, not very muscular and situated outside the proboscis. The thickness of the buccal mass wall differs only slightly from that of the buccal tube. An alteration of muscle structure of the wall occurs far from the venom gland opening, as if the venom gland

TABLE 2. — List of characters and states used in cladistic analysis.

1. Epithelium of posterior rhynchodeal wall: 0, glandular; 1, not.
2. Proboscis length: 0, long; 1, short.
3. Proboscis wall thickness (in % of proboscis diameter): 0, more than 10%; 1, less than 10%.
4. Proboscis tip: 0, typical; 1, *Comitas*-like.
5. Epithelial pad at tip of buccal tube: 0, present; 1, absent.
6. Anterior buccal tube sphincters: 0, one; 1, two; 2, absent.
7. Sac-like enlargement of the buccal tube: 0, present; 1, absent.
8. Shifting buccal tube sphincter: 0, absent; 1, present.
9. Buccal lips: 0, absent; 1, uninvertible; 2, invertible.
10. Position of the buccal mass: 0, within the proboscis; 1, posterior to the proboscis base; 2, at the proboscis base.
11. Buccal mass sharp: 0, not curved; 1, curved.
12. Elongation of the oesophagus: 0, absent; 1, present.
13. Increasing of the oesophagus diameter: 0, absent; 1, present.
14. Salivary glands: 0, acinous; 1, anastomosing tubular; 2, modified acinous.
15. Venom gland duct: 0, present; 1, absent; 2, modified.
16. Position of opening of venom gland into oesophagus: 0, at the border of buccal mass; 1, behind buccal mass.
17. Number of muscular layers of the muscular bulb: 0, three layers with the connective tissue; 1, one or two layers without connective tissue.
18. Orientation of fibres in outer two layers of muscular bulb: 0, similar orientation; 1, opposite orientation.

opens in the middle of the buccal mass. Buccal lips are large and muscular, with a very narrow space between them. The radular sac has a wide opening, and the buccal sac is absent. Salivary ducts are short, straight and open on both sides of radular sac. Salivary glands are very small and acinous. The venom gland opens near the radular sac opening, with a very small duct. The venom gland histology does not change along its length. The muscular bulb is composed of two layers of large longitudinal muscles separated by a layer of unstructured connective tissue, with an innermost layer of circular fibres. All muscle fibres are very thin. The lumen of the muscular bulb is rather wide. The oesophagus is medium elongated. Oesophagus diameter does not increase behind the nerve ring.

CLADISTIC ANALYSIS AND RELATIONSHIPS WITHIN THE SUBFAMILY

The analysis was based on 18 characters recognized in previous works on Conoidea (Taylor *et al.* 1993; Kantor *et al.* 1997) (Table 2). Some characters were somewhat changed, taking into account the peculiarities of the given subfamily: **Character 3.** The ratio between the proboscis wall thickness and the proboscis diameter appear-

ed to be important in distinguishing some species, which possess a large proboscis, but the wall thickness does not exceed 10% of diameter, and there are large longitudinal muscles passing along the buccal tube.

Character 4. It emphasizes the presence of a thin-walled stalk at the proboscis apical end in some species.

Character 8. It considers that group of sphincters which cannot be assigned neither to anterior nor to posterior (see Discussion).

Character 13. It considers the sharp alteration in the histological structure of the oesophagus wall in some species.

Character 15. An additional state two was introduced for *Marshallena philippinarum* whose venom gland changes its histology far behind the nerve ring whilst the duct is apparently absent.

The data on some species of *Aforia* Dall, 1889 were incomplete, because only the very anterior parts of digestive system were sectioned.

The analysis was performed with *Gemmula deshayesi* (Doumet, 1839) taken as an outgroup (Table 3). The data on this species were extracted from Kantor *et al.* (1997). Characters 4, 8, 13, 14 and 16 were treated as ordered.

A heuristic search produced 12 equally parsimonious trees (47 steps, consistency index = 0.489, retention index = 0.718, homoplasy index =

TABLE 3. — Distribution of character states for the cochlespirine gastropods examined. Details of characters are listed in Table 2.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<i>Gemmula deshayesi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Aforia inoperculata</i>	?	1	0	0	1	1	0	0	2	1	1	?	?	?	1	1	?	?
<i>Aforia circinata</i>	0	0	0	0	1	0	0	0	1	2	0	0	1	0	1	1	1	1
<i>Aforia lepta</i>	1	1	0	0	1	2	1	0	1	2	0	0	1	0	1	0	1	1
<i>Aforia moskalevi</i>	?	0	0	0	1	1	0	0	1	2	0	1	1	0	1	1	1	1
<i>Aforia aulaca alaskana</i>	?	0	0	0	1	1	0	0	1	2	?	?	?	?	?	?	?	?
<i>Aforia crebristriata</i>	?	0	0	0	1	1	0	0	1	2	0	0	1	0	1	1	1	1
<i>Aforia abyssalis</i>	?	1	0	0	0	1	0	0	1	2	0	1	1	0	1	1	1	1
<i>Aforia kupriyanovi</i>	?	1	0	0	0	1	0	0	1	2	?	?	?	?	?	?	?	?
<i>Antiplanes sanctioannis</i>	0	0	0	1	0	2	0	1	1	2	0	1	1	0	1	0	1	0
<i>Carinoturris polycaste</i>	0	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0
<i>Cochlespira pulchella</i>	0	0	0	0	0	1	0	0	2	1	1	1	0	0	1	1	1	1
<i>Cochlespira radiata</i>	0	0	0	0	0	1	0	0	2	1	1	1	0	0	1	1	1	1
<i>Comitas murrawolga</i>	0	0	1	1	0	2	0	1	2	1	0	1	0	0	1	0	1	0
<i>Comitas onokeana vivens</i>	0	0	1	1	0	2	0	1	0	1	0	1	0	0	1	0	1	0
<i>Kurilohadalia elongata</i>	0	0	1	0	1	1	0	0	1	1	0	0	0	1	0	0	0	0
<i>Leucosyrinx pyramidalis</i>	0	0	0	0	1	1	0	0	2	1	1	1	1	0	1	1	1	1
<i>Leucosyrinx verilli</i>	0	0	1	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0
<i>Marshallena philippinarum</i>	0	0	0	1	1	2	1	1	1	1	1	0	0	0	2	0	1	?
<i>Megasurcula carpenteriana</i>	1	0	1	0	1	1	0	0	0	1	1	1	0	0	0	0	?	?
<i>Plicisyrinx decapitata</i>	0	0	1	0	1	0	1	0	1	2	0	1	0	2	0	0	0	0

0.511). The trees were rather uniform, and most branches were supported in all trees. The resolution of the analysis was poor mostly in branches, consisting of numerous species of *Aforia* and in that including two nearly identical morphologically species of *Cochlespira*. This, however, seems rather natural, because anatomical data used in the analysis, usually do not allow to distinguish species of a genus.

A strict consensus tree is shown in Figure 15.

TABLE 4. — Synapomorphies for interior nodes. Nodes numbered as in Figure 15.

Node	Synapomorphies (Character: state)
1	3(1)
2	9(1)
3	5(1)
4	9(1), 14(1)
5	15(1), 17(1)
6	4(1), 6(2), 8(1)
7	3(1)
8	16(1), 18(1)
9	10(2)
10	5(1)
11	2(1)
12	9(2), 11(1)
13	5(1)

The synapomorphies for internal nodes are listed in Table 4.

The main result of the analysis was the division of the taxa studied into three large groups, which correspond well to those based on estimation of key anatomical peculiarities (see below). These groups may represent different evolutionary lineages within the Cochlespirinae, but any taxonomic conclusions seem to be premature, due to a rather small percentage of cochlespirine genera covered by the study.

DISCUSSION

ANATOMICAL VARIATION

The subfamily Cochlespirinae is not very diverse in foregut morphology. It is possible to recognize three types of the foregut organization. The most important characters are the position and structure of venom gland with muscular bulb, while all other characters, such as the position and structure of buccal mass, the buccal lips, the salivary glands, and the sphincters of buccal tube are either uniform (e.g., salivary glands), or too variable, even within the genus (e.g., the number of buccal tube sphincters). Therefore, the ana-

lysis of structure of the whole digestive system may be based only on the complex of characters. The presence of glandular epithelium in the rhynchodeum is characteristic of the majority of cochlespirines, except *Aforia lepta* and *Megasurcula carpenteriana*. The same concerns the protraction of proboscis, which is permitted by eversion of the posterior part of rhynchodeum. The rhynchodeum walls in the posterior part are not attached to the body walls. During the proboscis protraction, they move together with the proboscis and become the continuation of its walls, thus making the proboscis substantially longer. In most cases, excepting most *Aforia* species, there is also a loop of oesophagus situated behind the buccal mass but anterior to the nerve ring. The presence of the loop is connected with proboscis protraction and provides an additional length to avoid the passage of structures, situated behind the nerve ring, through the ring during the proboscis protraction (Ponder 1973). The proboscis is usually long, except in some species of *Aforia*. The latter, however, usually possess a loop of oesophagus, which may indicate that the proboscis is in a retracted position.

The structure of the apical part of the proboscis is rather variable. No species of Cochlespirinae was found to possess intermediate or posterior sphincters. Anterior sphincters may be absent, as in *Aforia lepta*; all other species studied possess either one (e.g. *Aforia circumata*, *Plicisyrinx decapitata*, *Marshallena philippinarum*, *Antiplanes sanctioannis*), or two anterior sphincters. The sac-like enlargement of buccal mass is usually present, except in three species (*Plicisyrinx decapitata*, *Aforia lepta*, and *Marshallena philippinarum*), while the epithelial pad is present in only half of the examined species. Different combinations may be found within a genus and even subgenus and, as in other subfamilies (Taylor *et al.* 1993; Kantor *et al.* 1997), there is no correspondence with other anatomical characters of the foregut.

The apical part of the proboscis is of special interest in four species: *Comitas murrayolga*, *C. onokeana*, *Antiplanes sanctioannis* and *Marshallena philippinarum*. In this group of species the proboscis narrows abruptly in the apical part. This results in the formation of a thin stalk

which is a continuation of the proboscis and is two to four times longer than the radular tooth length. Inner and outer walls of the stalk are very thin, bilayered, formed by longitudinal and circular muscles, and lined with the same epithelium. The wider part of the proboscis contains one or two buccal sphincters (all species), a sac-like enlargement (*Comitas* Finlay, 1926) and an epithelial pad (*Comitas* and *Antiplanes sanctioannis*). In both species of *Comitas*, at some distance from the stalk the external columnar epithelium abruptly changes to a lower cubic epithelium, identical to the inner epithelium of the buccal tube (Fig. 5A, B). There is no such change in the epithelium in *Antiplanes* and *Marshallena*, though in *Antiplanes* the columnar epithelium of the outer proboscis wall gradually transfers into the cubic one on the outer wall of the stalk.

The stalk may vary in length in different specimens of *Comitas* and *Antiplanes*. When the stalk length changes, the position of buccal sphincters in relation to the proboscis tip also changes (Fig. 5A, B). The distance from the sphincter to the proboscis tip is about four radular tooth lengths in Figure 5B, whereas it is about two tooth lengths in Figure 5A. Figure 6 shows a specimen of *Antiplanes* with the longest stalk, when the sphincters are most close to the proboscis tip and the buccal mass lies inside the proboscis base. Another specimen of *Antiplanes* (not figured) had a shorter stalk, the distance between sphincters and the proboscis tip was greater, and the buccal mass was shifted from the proboscis base outwards.

It is problematic to ascribe these sphincters to a category. It was suggested to designate sphincters as anterior if the distance from a sphincter to the mouth opening does not exceed 2.5 tooth lengths (Kantor *et al.* 1997). In the situation under consideration, the position of sphincters may vary, taking either anterior or posterior position. Nevertheless, the presence of a sac-like enlargement and an epithelial pad indicates that the sphincters are used for the tooth fixation and, therefore, are functionally anterior. Such sphincters, varying in position but functioning as anterior, are designated here as shifting sphincters.

When discussing the structure of anterior part of

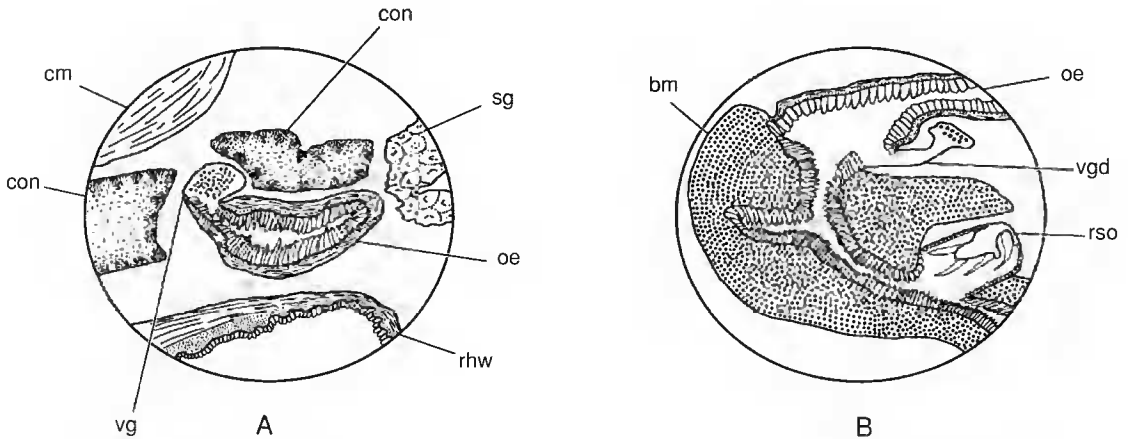


FIG. 13. — A, *Cochlespira pulchella*, oesophagus portion near the nerve ring, with the venom gland opening; B, *Megasurcula carpenteriana*, buccal mass, with the opening of the venom gland duct.

the proboscis, we avoided the use of the term "mouth", because it is defined functionally and, in this case, does not coincide with anatomical tip of the proboscis. The mouth is usually characterized by a change of outer epithelium of the proboscis wall for the inner epithelium of the buccal tube, and by an alteration of the wall muscular structure. Similar changes occur at the base of the stalk in the species considered. This fact and identity of the epithelium of inner and outer walls of the stalk with the epithelium of the rest part of the buccal tube allow to suggest that the stalk represents an everted part of the buccal tube. However, the absence of a distinct change in epithelium in *Marshallena philippinarum* does not permit to state reliably that the stalk is homologous in all four species.

The buccal mass may be situated either at the proboscis base or outside it. There are no species of Cochlespirinae examined which possess the buccal mass inside the proboscis. Buccal lips are absent in *Comitas onokeana vivens*, *Leucosyrinx verrilli* and *Megasurcula carpenteriana*, in all others they are present. Both species of *Cochlespira*, one of *Aforia*, *Leucosyrinx pyramidalis*, and *Comitas murrayolga* have inverted buccal lips. It is very interesting that in two *Comitas* species, one lacks the buccal lips, and another possesses inverted buccal lips. In other respects, these species are virtually identical to each other anatomi-

cally. This shows that the presence and the position of the buccal lips may not be good characters for the analysis of anatomy, and may vary even within a genus.

Salivary glands, except in two species, are the normal acinous type. Anastomosing tubular glands are present in *Kurilohadalia*, and the modified acinous type – in *Plicisyrinx*. These types of salivary glands were first described in the species of the subfamily Crassispirinae (Kantor *et al.* 1997).

The structure of the venom gland itself is similar in all the species studied, except *Marshallena philippinarum*. The venom gland does not change its histology in the passage through the nerve ring and opens directly or by a small duct in the oesophagus. The location of the venom gland opening correlates with the structure of muscular bulb. When the venom gland opens behind the buccal mass, the duct is absent and the muscular bulb is composed of two oppositely oriented muscle layers, with no connective tissue layer. When the venom gland opens at the buccal mass border, a very small duct may be present and the muscular bulb is composed of three muscle layers. Two outer layers have a similar orientation and are separated by a connective tissue layer. The venom gland may also open at the border of the buccal mass without a duct. In this situation the muscular bulb is usually composed of two

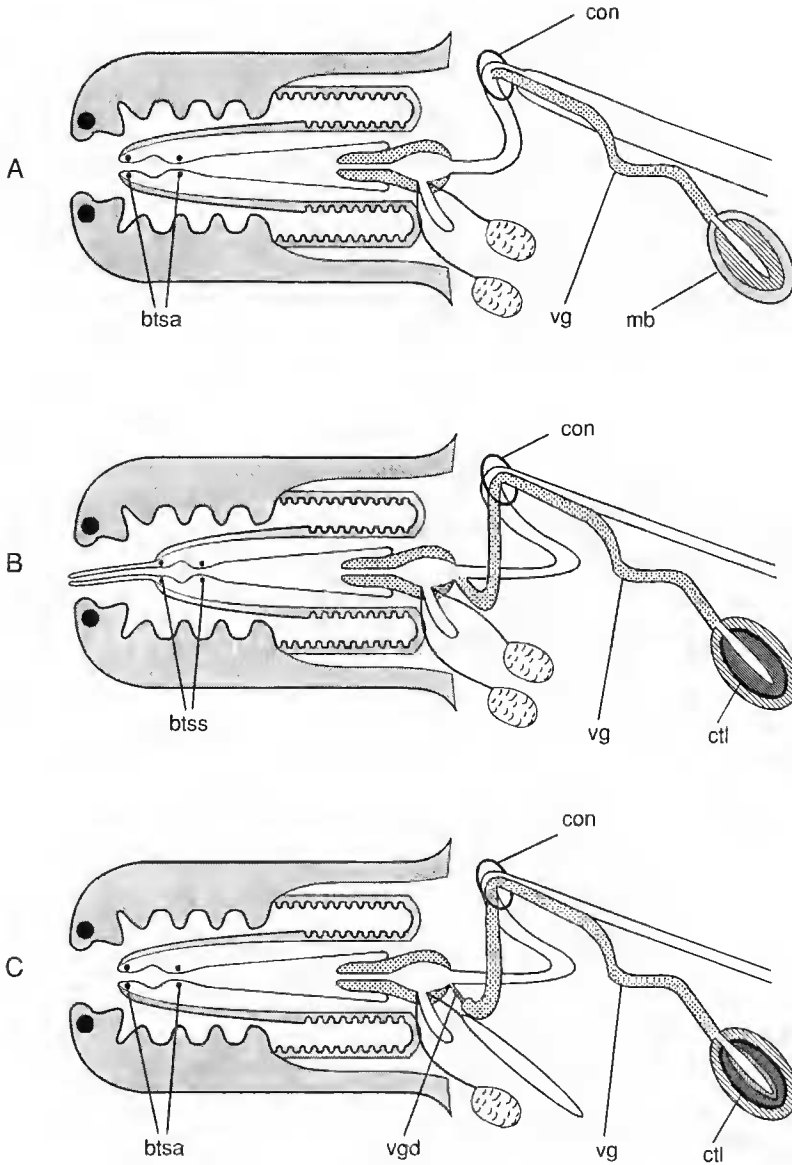


FIG. 14. — Types of foregut organization. **A**, *Aforia* spp., *Leucosyrinx pyramidalis*, *Cochlespira pulchella*, *C. radiata*; **B**, *Antiplanes sanctioannis*, *Marshallena philippinarum*, *Comitas onokeana vivens*, *Comitas murrayolga*; **C**, *Carinoturris polycaste*, *Kurilohadalia elongata*, *Leucosyrinx verrilli*, *Megasurcula carpenteriana*.

similarly oriented muscle layers, without a connective tissue layer (e.g. *Comitas* sp., *Antiplanes sanctioannis*). *Marshallena philippinarum* is the exception, possessing the muscular bulb composed of a single muscle layer and the venom gland of a very peculiar structure (see description).

It is necessary to define the term “venom gland duct” (Fig. 13A, B). We consider the venom gland duct being present if there is an abrupt narrowing before the opening and at least a small part of the gland lacks venom granules. If the venom gland has a large opening and the venom

granules are present just near the opening, we consider the venom gland duct to be absent. Observations herein suggest that the site and the mode of the venom gland opening, and the structure of the muscular bulb are closely interrelated and very important. In any case, it is now evident that if the venom gland duct is absent, the number of muscle layers of the muscular bulb is reduced to two (and even to one in *Marshallena*). When the venom gland duct is present, irrespective of its length, the muscular bulb is composed of three layers. For example, some Cochlespirinae (e.g. *Carinoturris polycaste*, *Kurilohadalia elongata*, *Leucosyrinx verrilli*, *Megasurcula carpenteriana*, *Plicisyrinx decapitata*) have a very short duct, whereas all Crassispirinae (Kantor *et al.* 1977) have a long duct, and a very similar three-layer structure of the muscular bulb.

As stated above, one of the most important criteria in distinguishing the three morphological groups in Cochlespirinae unexpectedly became the structure of the venom gland and the muscular bulb, though similarities and distinctions in the foregut organization should be also taken into account.

The first group includes 11 species. The principal characters are the position of the venom gland opening (beyond the buccal mass) and the structure of the muscular bulb composed of two oppositely oriented muscle layers (Fig. 14A). This group consists of *Aforia* spp., *Leucosyrinx pyramidalis*, *Cochlespira pulchella*, *C. radiata*. The three latter species have a well-developed oesophageal loop and the distance from the buccal mass to the nerve ring and, correspondingly, to the place of the venom gland opening is rather long. In all species of *Aforia* this distance is shorter. In fact, some *Aforia* species (e.g., *A. moskalevi*, *A. abyssalis*) have an oesophageal loop but it is not very long. In *A. circumnata* and *A. crebristriata*, the distance between the buccal mass and the nerve ring is very short. However, in all *Aforia* species the nerve ring is situated at the same level as the buccal mass, but laterally. As a result, the oesophagus curves behind the buccal mass and passes along the buccal mass for some distance. Thus even in species lacking the oesophageal loop, the oesophagus deviates from the

buccal mass at an angle of about 90°. In many species (e.g. *Leucosyrinx pyramidalis*, *Aforia circumnata*, *A. leptia*), the end of the buccal mass is not clearly differentiated histologically. The buccal mass wall gradually becomes thinner, almost without a change in histology. A distinct change occurs only near the nerve ring and behind it, where oesophagus diameter greatly increases. This increase is characteristic of *Leucosyrinx pyramidalis* and all *Aforia* species, including those having a well-differentiated buccal mass.

The position of the venom gland opening behind the buccal mass is probably the result of an elongation of oesophagus at the expense of the rear part of the buccal mass. This may be evidenced by the absence of clearly differentiated post-anterior end of the buccal mass in some species. It is possible to assume that the buccal mass itself extends to the nerve ring, and the oesophagus expansion after the ring with the changing oesophagus wall histology represents the end of the buccal mass. However, both species of *Cochlespira*, which are superficially very similar to *Aforia*, have a well-differentiated buccal mass, a long oesophagus loop, and lack the oesophagus expansion behind the nerve ring. That is, in these species the elongation of oesophagus took place, but it occurred between the buccal mass and the venom gland opening.

Aforia leptia is a special case, because it completely lacks an oesophageal loop, its venom gland opens at the end of the buccal mass, and the nerve ring is situated just behind. However, the muscular bulb is also composed of two oppositely oriented layers, and the oesophagus expansion is present. This type of structure looks very peculiar, but it is necessary to take into account that the original description (Sysoev & Kantor 1987) was based on a single juvenile specimen, and it cannot be excluded that there may be rather substantial ontogenetic changes.

The second group consists of *Antiplanes sanctioannis*, *Comitas murraywolga*, *C. onokeana vivens*, and *Marshallena philippinarum*, with the latter species occupying a special position. This group is characterized by the structure of the muscular bulb composed of two muscular layers with similar orientation (or one muscular layer in *Marshallena philippinarum*); and the venom

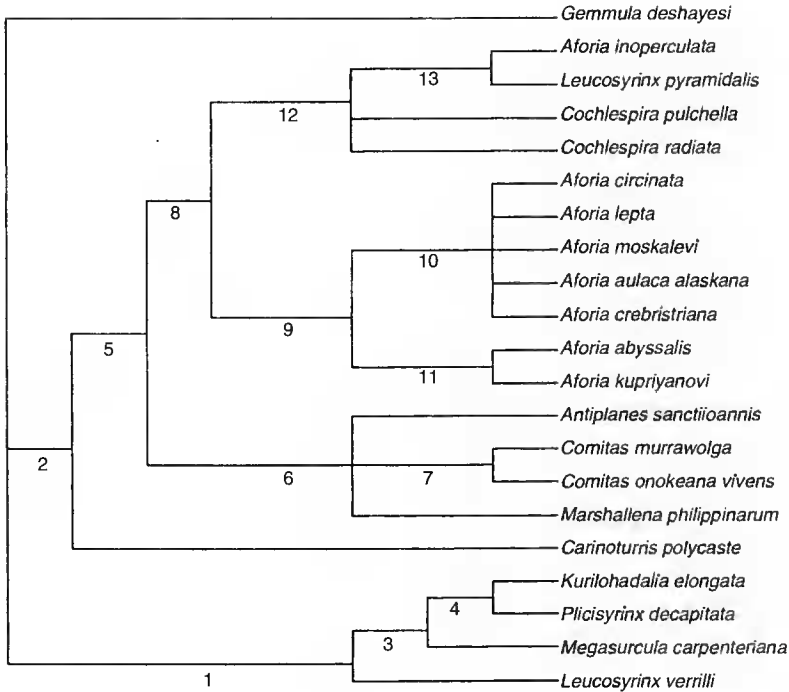


FIG. 15. — Strict consensus tree.

gland opening at the boundary of the buccal mass, without a duct (except in *Marshallena philippinarum*) (Fig. 14B). An additional character is the structure of the proboscis apical part, with a stalk and shifting sphincters. *Marshallena philippinarum* was assigned to this group for several reasons. In spite of the unique structure of the venom gland (see description) and the presence of only one layer in the muscular bulb, the latter is very similar to that of all other species of this group, and the structure of the apical end is also approximately the same.

The third group includes *Carinoturris polycaste*, *Kurilohadalia elongata*, *Leucosyrinx verrilli*, *Megasurcula carpenteriana*, and *Plicisyrinx decapitata* (Fig. 14C). These species have no clearly

expressed features, and cannot be assigned to the two other groups. In general, besides the three-layered muscular bulb with very large muscle fibres, they are characterized by a weakly coiled proboscis with a large and uniform diameter. The proboscis diameter is mostly occupied not by walls (less than 10% of the total diameter) but by longitudinal muscle bunches. The venom gland does not change its histology and opens by a small duct at the border of the buccal mass. The muscular bulb is composed of three muscular layers, two outer having a similar orientation and separated by a layer of connective tissue. The exception is *Carinoturris polycaste*, which possesses a very thin proboscis wall. Its muscular bulb is composed by very thin fibres. The size of

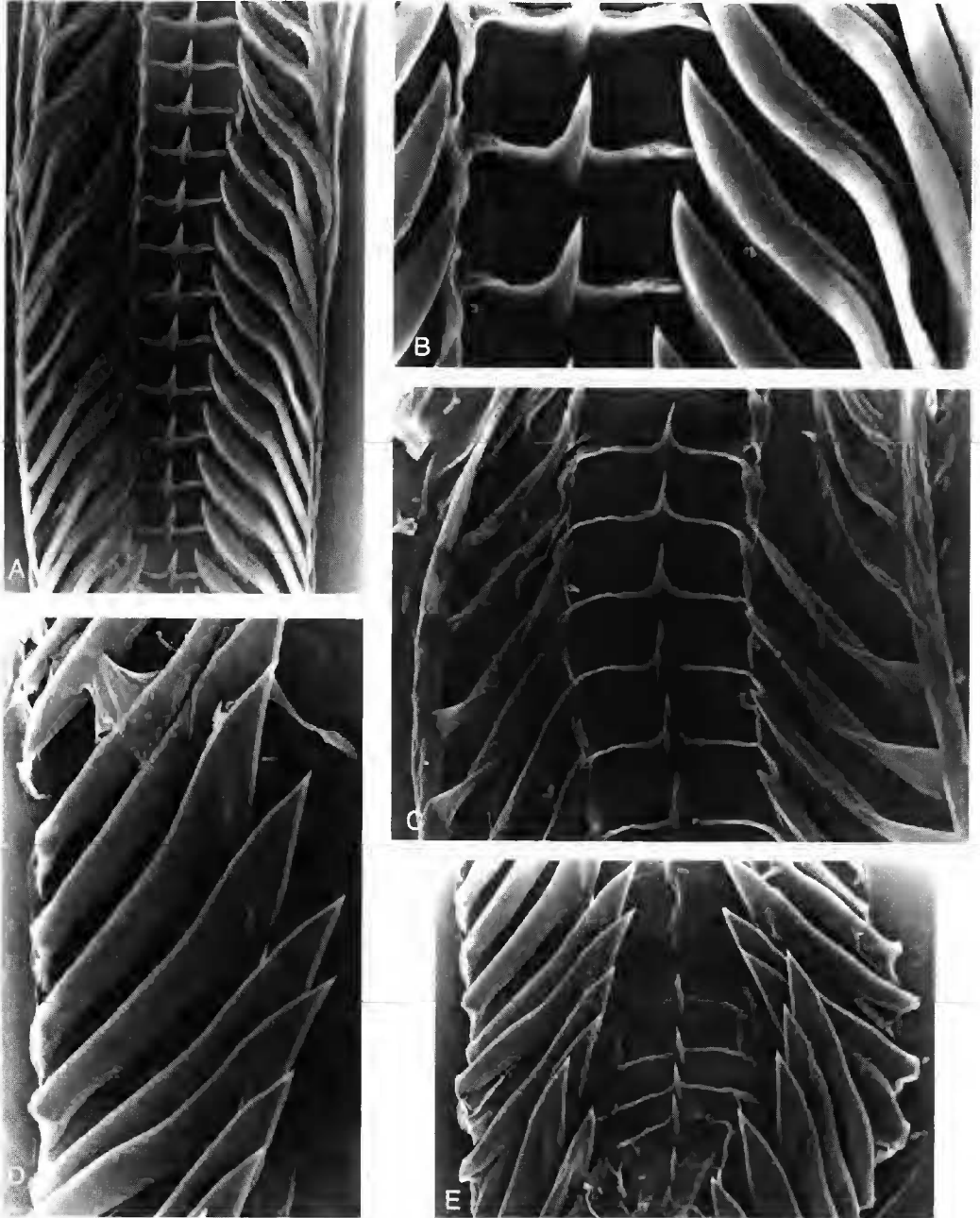


FIG. 16. — Radulae of Cochlespirinae. A, B, *Cochlespira pulchella*; C, *Cochlespira radiata*; D, E, *Leucosyrinx (Sibogasyrinx) pyramidalis*.

the fibres is very important, as it will be shown below. Other types of salivary glands also occur in this group, i.e. anastomosing tubular in

Kurilohadalia elongata and modified acinous in *Plicisyrinx decapitata*, previously recorded in the Crassispirinae (Kantor *et al.* 1997).

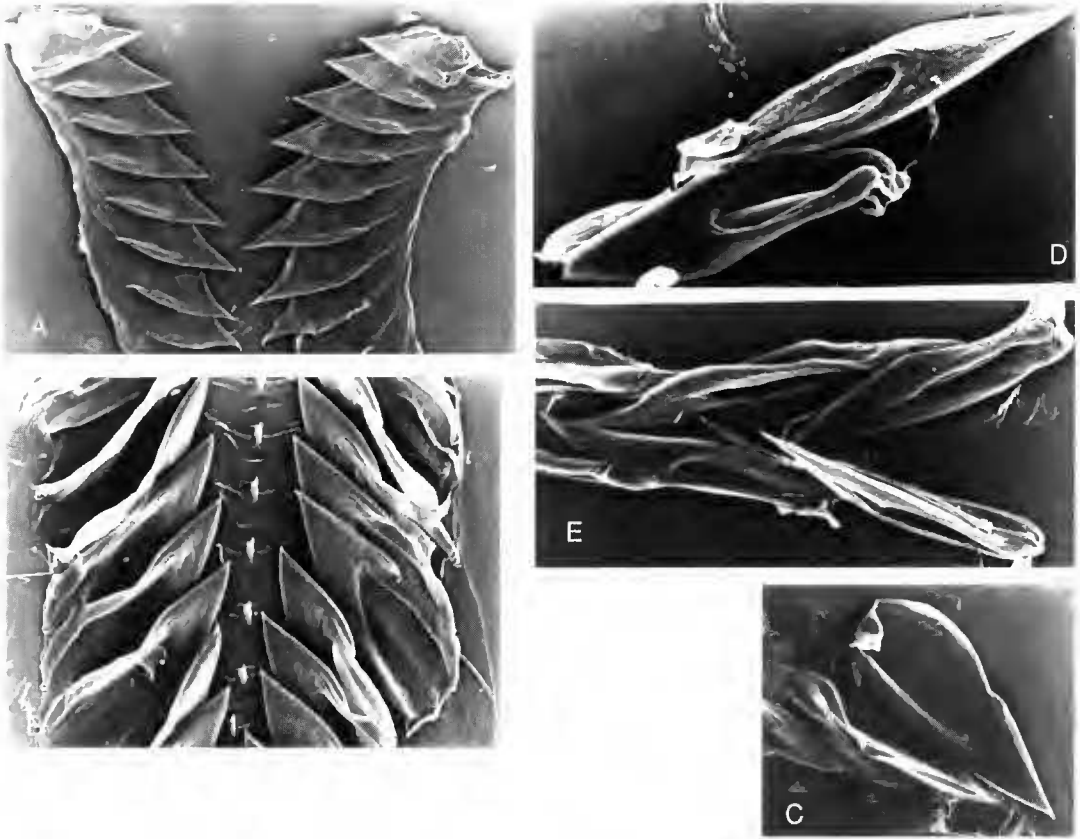


FIG. 17. — Radulae of Cochlespirinae. A, *Comitas onokeana vivens*; B, *Comitas murrawolga* - middle part; C, *Comitas murrawolga*, initial part; D, E, *Marshallena philippinarum*.

SHELL AND RADULAR MORPHOLOGY

Shell characters appeared to be rather poorly correlated with features of foregut anatomy. It may be only mentioned that members of the first group, separated by anatomical characters and in the cladistic analysis, possess a typical cochlespirine elongated fusiform shell with a long anterior canal and weak axial sculpture. Species of the second group have stouter shells with shorter canals and well-developed sculpture (except for *Antiplanes*). The third group is very heterogeneous in shell characters corresponding to the wide anatomical variation. However, no shell character was found to strictly correlate with a feature of the foregut anatomy, or a set of anatomical characters.

The radular morphology of cochlespirines had

previously been assigned to the wishbone tooth type (Taylor *et al.* 1993). Robust, short, and curved marginal teeth with a knife-like cutting edge were found in *Antiplanes sanctioannis* (Kantor & Sysoev 1991; Taylor *et al.* 1993). Teeth of *Aforia* spp. (Sysoev & Kantor 1987) are similar to teeth of *Antiplanes*.

Among the species studied, more or less typical wishbone teeth were found in *Leucosyrinx pyramidalis* (Fig. 16D, E) and *Marshallena philippinarum* (Fig. 17D, E). They are quite comparable to the marginal teeth of many Crassispirinae (e.g. *Inquisitor*- and *Hindsiclava*-type teeth — see Kantor *et al.* 1997).

At the same time, the marginal teeth of both species of *Comitas* studied seem to be not true wishbone. At an early stage of formation, they

resemble a broad flat plate thickened apically and on outer sides (Fig. 17C). Later, the teeth become more similar to wishbone: the lateral thickenings become more distinct and appear like the separate limbs of a typical wishbone tooth. This process is more pronounced in *C. murrawolga* (Fig. 17B, C), whereas in *C. onokeana* the teeth remain flat and poorly differentiated (Fig. 17A). Nevertheless, a complete separation of tooth limbs does not occur in any of *Comitas* species.

The teeth of species of *Cochlespira* are somewhat different. In *C. pulchella*, they are of a normal wishbone form, with a narrow limb (Fig. 16A, B) whereas the teeth of *C. radiata* (Fig. 16C) consist of a longitudinally folded plate, forming a central canal, and resemble enroled hollow teeth, recognized by Taylor *et al.* (1993) for *Pilsbryspira*. It may be also added that the diversity of *Cochlespirina* teeth seems to be rather high, as indicated by drawings of radula of different species (Powell 1966: figs 17-20).

The central tooth may be variously developed: from a well-formed plate, with a strong cusp and clearly defined boundaries, as in *Cochlespira* (Figs 16A-C), to a weak formation, which looks like a membranc fold rather than a tooth (e.g., *Comitas onokeana*, fig. 17A). It should be mentioned that the central part of the radula of *C. onokeana* at early stages of formation shows two separate plates instead of a single tooth. This may indicate that the central "tooth" is actually a product of fusion of two teeth, and supports the idea of Kantor & Sysocv (1991) on the origin of central tooth in *Antiplanes*.

No correlation was found between the anatomy of digestive system and radular morphology in any of the species studied.

COMPARISON WITH OTHER SUBFAMILIES OF TURRIDAE

This article is the second in the series of works concerning Turridae, and in the first paper (Kantor *et al.* 1997) short descriptions of all subfamilies were given. Therefore, here we will mainly compare the two conchologically similar and best studied subfamilies: *Cochlespirinae* and *Crassispirinae*.

The subfamily *Crassispirinae* is characterized by very diverse structure of proboscis, buccal mass, and salivary glands. The proboscis structure is so variable not only within the subfamily, but even within the genera and subgenera, that a total of 13 types of foregut organization have been recognized. The most characteristic features of the subfamily are as follows: the presence of the rhynchodeum glandular epithelium, the ability of the rear part of rhynchodeum to evert during the proboscis protraction, the position of the oesophagus elongation usually between the buccal mass and the nerve ring, with a more or less long oesophagus loop, the presence of non-glandular venom gland duct, and the change in its histology behind the nerve ring, the presence of three-layered muscular bulb, with a layer of connective tissue (the bulb is composed by small fibres and the two outer layers have a similar orientation) (Taylor *et al.* 1993; Taylor 1994; Kantor *et al.* 1997).

The first two characters are present also in *Cochlespirinae*. Thus, the most characteristic features of this family become as follows: the absence of change in the venom gland histology behind the nerve ring in all groups; the complete absence of venom gland duct and, correspondly, the two-layered muscular bulb, without any connective tissue, or the presence of a small duct and the three-layered muscular bulb, like in *crassispirines*. In *cochlespirines* the muscular bulb, with a similar organization and arrangement of muscle layers, is composed of very large fibres, distinguishable even at a small magnification, whereas in *crassispirines* they are very small and form a compact layer.

Representatives of both subfamilies are rather well distinguishable conchologically, when typical forms are considered. Species of the subfamily *Crassispirinae* are generally characterized by a small claviform shell with a rather well-developed sculpture, while the shell of typical *cochlespirines* is fusiform, with a long anterior canal and a rather weak sculpture. But many representatives (e.g., *Plicisyrinx*) represent intermediate variants in conchological characters, and it is thus difficult to separate reliably these subfamilies only by the shell.

Anatomy of six species of *Clavatulinae* has been

described: *Turricula nelliae spurius* (Hedley, 1922), *Turricula javana* (Linnaeus, 1767), *Toxiclionella umida* (Sowerby, 1870), *Clionella sinuata* (Born, 1778), *Clavatula caerulea* (Weinkauff, 1875), *C. muricata* (Lamarck, 1822) (Kantor 1990; Taylor 1985, 1994; Taylor *et al.* 1993). The main difference of Clavatulinae from Cochlespirinae and all other turrid subfamilies is the position of the buccal mass inside the proboscis, near the mouth. As in Cochlespirinae, the buccal sphincters in Clavatulinae may be either present or absent. Oesophageal loop is similar to that in some Cochlespirinae and Crassispirinae. Venom gland opens in the buccal mass. The structure of muscular bulb is somewhat different from that in Cochlespirinae: the bulb is composed of two similarly oriented layers, with a connective tissue between layers.

A detailed comparison with Turrinae is currently rather difficult, due to insufficient data on this subfamily. Features characteristic of Turrinae often occur also in Cochlespirinae. For example, oesophageal loop may be absent, venom gland does not change its histology anterior to the nerve ring and opens at the buccal mass boundary by a short duct. However, the structure of muscular bulb differs from that found in all Cochlespirinae: its bulb is composed of two similarly oriented layers, with a connective tissue between layers. Another distinguishing character of Turrinae is the rhynchodeum lined with glandular epithelium along its entire length (Leviten 1970, *cit. after* Taylor *et al.* 1993; Taylor *et al.* 1993; Taylor 1994).

SYSTEMATIC CONCLUSIONS

The data obtained confirm that the main part of the subfamily Cochlespirinae represents an anatomically distinct group, differing from other subfamilies of Turridae in several minor but constant characters. At the same time, the subfamily in its currently adopted volume seems not to constitute a monophyletic group.

A special note should be made on the systematic position of the five species belonging to the third anatomical group. The cladistic analysis showed that four of the five species (*Kurilohadalia elon-*

gata, *Leucosyrinx verrilli*, *Megasurcula carpenteriana*, and *Plicisyrinx decapitata*) are clearly separated in all cladograms, whereas *Carinoturris polycaste* occupies an isolated position and is a sister-group of all species from the first and second anatomical groups. The group of the four species is defined on the cladogram by a single synapomorphy (relatively very thin walls of the proboscis), but evolutionary and functional significance of this character is unclear. In fact, the third anatomical group is somewhat intermediate in its morphology between Crassispirinae and Cochlespirinae and possesses some characters of both subfamilies. Conchologically, some of the taxa are also similar to representatives of both subfamilies and earlier were alternately referred to the Crassispirinae or to the Cochlespirinae (e.g. *Kurilohadalia* and *Plicisyrinx* – see above).

Two species of the genus *Leucosyrinx* were referred to different groups in both cladistic and anatomical analyses. These species belong to different subgenera: *Leucosyrinx* Dall, 1889 s. str. (*verrilli*, type species of the genus) and *Sibogasyrinx* Powell, 1969 (*pyramidalis*, type species of the subgenus). The great differences in anatomy indicate that these subgenera are not closely related, and the rank of the subgenus *Sibogasyrinx* should be raised to a full genus.

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